Father−offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal

Julien Mainguy, Steeve D. Côté, Marco Festa-Bianchet and David W. Coltman

References	This article cites 51 articles, 15 of which can be accessed free http://rspb.royalsocietypublishing.org/content/276/1675/4067.full.html#ref-list-1
Subject collections	Articles on similar topics can be found in the following collections behaviour (800 articles) ecology (929 articles) evolution (1104 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Proc. R. Soc. B* go to: **http://rspb.royalsocietypublishing.org/subscriptions**

Father–offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal

Julien Mainguy[1,*], **Steeve D. Côté**[1], **Marco Festa-Bianchet**[2] **and David W. Coltman**[3]

[1]*Département de biologie and Centre d'études nordiques, Université Laval, Québec, Québec, Canada G1V 0A6*
[2]*Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada J1K 2R1*
[3]*Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9*

In sexually dimorphic and polygynous mammals, sexual selection often favours large males with well-developed weaponry, as these secondary sexual characters confer advantages in intrasexual competition and are often preferred by females. Little is known, however, about the effects of sexually selected paternal traits on offspring phenotype in wild mammals, especially when considering that shared phenotypic traits and selection can also differ greatly between genders. Here, we conducted molecular parentage analyses in a long-term study population of mountain goats (*Oreamnos americanus*), an ungulate exhibiting high sexual dimorphism in mass, to first assess the determinants of yearly reproductive success (YRS) in males. We then examined the effects of paternal characteristics on offspring mass at 1 year of age. Paternity was highly skewed, with 9 per cent of 57 males siring 51 per cent of 96 offspring assigned over 12 years. Male YRS increased with age until apparent reproductive senescence at 9 years, but mass was a stronger determinant of siring success than age, horn length or social rank. Mass of sons increased with paternal mass, but the mass of daughters was negatively related to that of their father, a finding consistent with recent theory on intralocus sexual conflict. Because early differences in mass persisted to early adulthood, sex-specific effects of paternal mass can have important fitness consequences, as adult mass is positively linked with reproduction in both sexes. Divergent father–offspring phenotypic correlations may partly explain the maintenance of sexual dimorphism in mountain goats and the large variance observed for this homologous trait within each gender in polygynous mammals.

Keywords: body mass; genetic paternity; intralocus sexual conflict; offspring phenotypic quality; sexual selection; ungulates

1. INTRODUCTION

Sexual selection in polygynous mammals generally favours males with well-developed secondary sexual characters such as large body mass (Lidgard *et al.* 2005; Fisher & Cockburn 2006) and prominent weaponry (Coltman *et al.* 2002; Kruuk *et al.* 2002). Such developed traits generally confer advantages in intrasexual competition for access to females (Pelletier & Festa-Bianchet 2006). Sexual selection may also act on male traits through female choice, as preference for males with exaggerated secondary sexual characters can provide indirect genetic benefits to females that stem from (i) the coevolution between male traits and female choice (the 'sexy-son' hypothesis) and (ii) fitness-linked paternal alleles (the 'good-genes' hypothesis, see Andersson & Simmons 2006). Females probably value these potential indirect benefits, as they sometimes spend energy seeking high-quality males (Byers *et al.* 2005), may delay oestrus in their absence (Komers *et al.* 1999) and can even compete

for them (Bro-Jørgensen 2002). Sexual differences in the effects of body and weapon size on reproduction, however, may favour a reduced expression of these exaggerated traits in females (Bouteiller-Reuter & Perrin 2005). Sexually divergent selective pressures are thus widely considered as the source of the sexual-size dimorphism observed in most polygynous mammals (Weckerly 1998).

Genes coding for homologous traits such as body mass are shared by males and females, but phenotypic optima for these traits often differ greatly between genders. This has the potential of generating a 'tug-of-war' between parental alleles in offspring of sexually dimorphic species, a phenomenon known as intralocus sexual conflict (Bonduriansky & Rowe 2005; Bonduriansky & Chenoweth 2009; Cox & Calsbeek 2009). Maternal and paternal alleles are therefore expected to have sex-specific effects on offspring phenotype, with theory predicting reduced trait heritability for offspring of the opposite sex to that of the parent (Day & Bonduriansky 2004). The negative genetic correlation for fitness between the sexes reported in *Drosophila* (Chippindale *et al.* 2001) and in red deer (*Cervus elaphus*, Foerster *et al.* 2007) probably reflects this phenomenon in which males exhibiting high

reproductive success sire daughters with low reproductive success (Bonduriansky & Chenoweth 2009). A potential underlying reason for this observation is that the reproductively advantageous phenotype of a male may be coded by alleles that are maladaptive when expressed in a female, yielding daughters with reproductively disadvantaged phenotypes. Intralocus sexual conflict can thus have important fitness implications for females, as the indirect genetic benefits of selecting reproductively successful males as mating partners may be lost when a daughter is produced (Fedorka & Mousseau 2004). Phenotypic evidence of parent–offspring diverging patterns based on gender, however, is scarce (Calsbeek & Bonneaud 2008), despite being of great interest in evolutionary biology. If parental alleles affect progeny fitness differently according to gender, sexual selection may be substantially weakened, which can in turn maintain the variation observed in fitness-linked traits.

Here, we combined field observations and genetic parentage analyses from a long-term study of a wild sexually dimorphic ungulate, the mountain goat (*Oreamnos americanus*), to first assess which male traits (age, mass, horn length and social rank) affected reproductive success. We then examined whether paternal phenotype had an apparent influence on offspring phenotype when accounting for other sources of variation, and more specifically whether it differed according to offspring gender. In adult mountain goats, males are much heavier than females (figure 1), whereas there is no dimorphism in horn length (Côté et al. 1998a), as opposed to many other ungulates (Poissant et al. 2008). This alpine ungulate exhibits a polygynous/polygamous mating system in which mature dominant males obtain most matings (Mainguy et al. 2008). Heavy males also allocate more time than light males to the courting of females (Mainguy & Côté 2008). Therefore, we expected body mass to be the most important trait affecting male reproductive success (Festa-Bianchet & Côté 2008). We also expected reduced phenotypic correlations for body mass, a shared phenotypic trait commonly used as a measure of individual quality in ungulates (Gaillard et al. 2000; Røed et al. 2007), between parents and their opposite-sex progeny. Finally, we examined whether mass as a yearling, whether influenced by parental masses or not, was maintained until early adulthood.

2. MATERIAL AND METHODS

(a) Study area
We studied mountain goats at Caw Ridge (54° N, 119° W), west-central Alberta, Canada. This native mountain goat population uses approximately 28 km^2 of alpine grassy slopes, short cliffs and open subalpine forest at 1750–2170 m elevation. The population, studied intensively since 1989, has ranged from 81 to 159 individuals, with 98 per cent or more of individuals aged 1 year old or more marked since 1993. Further details about the study area are in Festa-Bianchet & Côté (2008).

(b) Captures, measurements and genetic sampling
Goats were captured from late May to mid-September 1986–2007 ($n = 756$ captures of 398 individuals) in remotely controlled box traps and self-tripping nylon mesh Clover traps baited with salt (Côté et al. 1998b). Goats 2
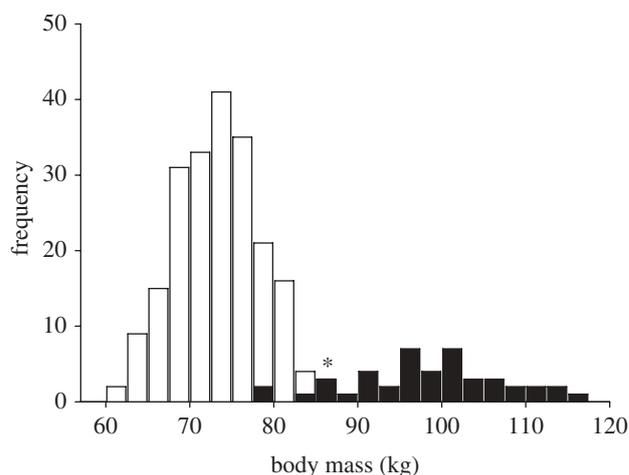

Figure 1. Body mass adjusted to 15 July for mountain goats aged 6 years or above at Caw Ridge, Alberta, Canada. Forty-four and 210 individual-year observations of 26 males (black bars) and 78 females (white bars) are shown, respectively. An overlapping, but identical frequency between sexes is indicated by an asterisk.

years or above were drugged via intramuscular injection of xylazine hydrochloride, later reversed by injection of ida-zoxan (Haviernick et al. 1998). All individuals were marked with plastic ear tags, visual or radio-collars. From 1994 to 2007, a tissue sample was taken from each captured goat using an ear punch, and kept in a solution of 20 per cent dimethylsulfoxide saturated with NaCl at −20°C. After 1997, kids were not captured owing to the risk of abandonment (Côté et al. 1998b). Goats that were adults when first captured were aged by the number of horn annuli (Côté et al. 1998a). The length of each horn was measured with a flexible tape (± 1 mm). Goats were weighed to the nearest 0.5 kg with a spring scale. Côté et al. (1998a,b) provide further details on capture procedures. Many goats were also weighed without handling in 2001–2007 ($n = 1331$ masses from 172 individuals aged 1 year or above) using one to three electronic platform scales baited with salt.

(c) Field observations
Goats were observed with spotting scopes (15–45×) almost daily from mid-May to mid-September 1989–2007 and during the rut (November and early December) in 2004–2006. For each group sighted, we noted the identity of all individuals and determined whether females were lactating by observations of nursing behaviour. During parturition in May and June, the study area was intensively searched each day to determine kid birth dates (Côté & Festa-Bianchet 2001a). Females produce up to one kid annually, generally starting at the age of 4 or 5 years and very rarely at age 3 years (Côté & Festa-Bianchet 2001b). Kids were sexed by the observation of the vulvar patch and by urination posture (Côté & Festa-Bianchet 2001c). Many mother–offspring pairs were determined when the yearling associated with its mother in the spring (Gendreau et al. 2005).

Males first participate actively in the rut at 3 years of age (Mainguy & Côté 2008), but most of the matings observed involved dominant males aged 6 years or more (Mainguy et al. 2008). Male social ranks were determined from interactions observed during the rut (Mainguy et al. 2008). Briefly, adult males were organized in annual dominance hierarchy matrices based on all-occurrence sampling of

agonistic encounters. All hierarchies were linear (Mainguy *et al.* 2008). As matrix size varied among years, we transformed social ranks as $1 - (rank/N_i)$, where N_i is the number of males in the matrix in year i (Côté 2000). Standardized ranks, therefore, ranged from 0 (subordinate) to 1 (dominant).

(d) Microsatellite genotyping

A total of 296 individuals, or 74 per cent of those marked and monitored since the beginning of the study, were sampled for genetic analyses. Genomic DNA extracted from ear tissue was PCR-amplified using 29 polymorphic microsatellite markers (Mainguy *et al.* 2005). Owing to the difficulty of amplifying and scoring locus BM121, each individual was genotyped at up to 28 loci with a genotyping success of 99.9 per cent.

(e) Parental assignments

Since the beginning of the study, 194 goats were behaviourally associated with a mother (Côté & Festa-Bianchet 2001*a*; Gendreau *et al.* 2005). We confirmed all but one of 111 maternal associations that could be tested genetically using the parentage-assignment software CERVUS 3.0 (Kalinowski *et al.* 2007). Using the same software, we inferred maternity for 81 additional goats for which mother identity could not be determined by field observations, following methods described in Mainguy *et al.* (2009). Among the 191 goats associated to a known genotyped mother, we inferred genetic paternity for 100 of them at strict (95%) statistical confidence (Mainguy *et al.* 2009). Only goats with known parents were considered to assess traits influencing male yearly reproductive success (YRS) and to investigate parent–offspring phenotypic correlations.

(f) Statistical analyses

We adjusted mass to 15 July according to the sex-specific growth rates of three age classes (yearlings, 2 year olds and adults; Côté *et al.* 1998*b*; Mainguy & Côté 2008). The mean of all adjusted masses was used for individuals weighed multiple times in the same year.

We modelled male YRS, defined as the number of offspring that survived to 1 June of the following year, using a generalized linear mixed model (GLMM) implemented with the GLIMMIX macro of SAS 9.1 (SAS Institute 2003) and a Poisson error structure with a log-link function. Variables considered in explaining variance in male YRS were male age, mass, horn length and social rank the year the yearling was sired, all fitted as continuous fixed effects. Male identity and year were fitted as random terms in this analysis to account for between-individual variance and differences in the number of yearlings assigned attributable to annual variations (Littell *et al.* 1998). In addition, we tested whether some within-individual variance occurred over time by exploring different covariance structures (e.g. first-order autoregressive) and comparing the pseudo-AIC values obtained when the same fixed effects were considered (Littell *et al.* 2000). The variance components structure for both male identity and year yielded the most parsimonious mixed-effect model and thus, within-individual variance was either low or non-existent in our dataset. As males are rarely captured after 4 years of age, but more than 93 per cent of their horn growth is completed by that age (Côté *et al.* 1998*a*), we used the length of the first three annuli of the longest horn as an index of horn length. Because male YRS could vary nonlinearly with age and mass, we also

included age^2 and mass^2 in the models. To avoid collinearity problems with their quadratic terms, age and mass were standardized by centring their mean on 0 when analysed within a same model.

To examine the effects of parental characteristics on offspring mass at 1 year of age, we first built two separate models that included either maternal or paternal age and mass (i.e. one-parent analysis), as we knew the mass of both parents for only 25 yearlings of 96 tested. The mass of the subset of yearlings assigned to both a mother and a father ($n = 43$ females and 45 males) did not differ from those of yearlings that were either only assigned to a mother or were unassigned ($n = 61$ females and 66 males) when accounting for sex-related differences (females: 33.0 ± 0.4 versus 32.3 ± 0.5 kg, males: 34.5 ± 0.5 versus 36.4 ± 0.5 kg, respectively; $F = 0.99$, d.f. = 194, $p = 0.32$). Similarly, birthdates did not differ between assigned (median birth date = 21 May, $n = 51$) and, maternally assigned (only) or unassigned yearlings (median birth date = 22 May; $n = 198$, Kruskall–Wallis test, $H = 2.37$, d.f. = 1, $p = 0.12$). Therefore, the subset of assigned yearlings was representative of the population. In parent–offspring analyses, parental age was considered because it has been shown to influence offspring traits in some vertebrates (Ellis *et al.* 2000; Hegyi *et al.* 2006), and maternal age in mountain goats of the same population was previously shown to affect positively the mass of their sons at 1 year of age (Gendreau *et al.* 2005). In each of the one-parent models, yearling sex and birth date were included as covariates, as yearling males are approximately 10 per cent heavier than females (Festa-Bianchet & Côté 2008), and early-born kids are heavier than late-born ones (Côté & Festa-Bianchet 2001*a*), a difference that could persist to 1 year of age. In all analyses of yearling mass, maternal characteristics were measured in the year of birth, whereas paternal characteristics refer to those in the preceding year when siring occurred. To test for reduced opposite-sex phenotypic correlations, the interactions between parental mass and yearling sex were included in a linear mixed model (LMM) with parent identity and year fitted as random terms to account for pseudoreplication. As for the analysis of male YRS, the variance component covariance structure with parent identity and year fitted as random terms was the most parsimonious among those explored. Using a backward procedure, variables were then dropped based on their *p*-value. Parental characteristics that explained a significant part of the variance in yearling mass or that were the last to be removed from the one-parent models were included in a single model, together with their interactions and those with yearling sex, to consider the potential influences of parental characteristics on offspring mass, as offspring phenotype is heritable through both parents.

To test whether differences in yearling mass were maintained until early adulthood, we used a generalized linear model (GLM) to compare adjusted masses at 1 and 3 years of age, the minimal age at which both sexes start to participate actively in the rut. By the age of 3 years males have reached approximately 63 per cent of asymptotic mass and females approximately 78 per cent (Mainguy 2008).

All analyses were conducted in SAS 9.1 (SAS Institute 2003). Statistical tests were two-tailed and significance level was set at 0.05. Inspection of residuals indicated no violation of the assumptions of normality and homoskedasticity when required. All means are presented ±s.e.

3. RESULTS

(a) *Parental assignments*

Ninety-six goats for which both parents were identified survived to 1 year. Of these, 51 per cent were sired by five of the 57 candidate fathers tested over 12 years. The mean number of yearlings assigned per male each year varied between 0.18 ± 0.12 and 0.71 ± 0.24. Each rut, only a few males were able to sire at least one and up to seven kids that survived to 1 year: 69 per cent of 215 'male–year' observations had no yearling assigned.

(b) *Male characteristics and reproductive success*

Male YRS peaked at 8 years and decreased afterwards (figure 2a), as revealed by the quadratic age term (age: $\beta = 0.09 \pm 0.01$, $F = 40.3$, d.f. = 146, $p < 0.0001$; age^2: $\beta = -0.014 \pm 0.004$, $F = 12.9$, d.f. = 146, $p = 0.0004$; $n = 215$ observations of 57 adult males over 12 years). The age-specific proportion of males that sired at least one kid followed the same pattern (figure 2a). When male mass, $mass^2$ and horn length were considered with age and age^2 in the same model, only mass was retained in the final model ($\beta = 0.09 \pm 0.01$, $F = 34.8$, d.f. = 31, $p < 0.0001$, figure 2b). When tested alone, horn length was not correlated with male YRS ($\beta = 0.02 \pm 0.02$, $F = 1.63$, d.f. = 124, $p = 0.20$). The effect of social rank on male YRS could only be tested for the ruts in 2004 and 2005. When tested alone, social rank had a positive influence on male YRS ($\beta = 4.74 \pm 1.28$, $F = 13.7$, d.f. = 5, $p = 0.01$; figure 2c). When age and mass were considered with rank in the same model without accounting for random effects owing to small sample size, however, rank was the first term to be removed ($\beta = 1.63 \pm 4.71$, $\chi^2 = 0.12$, d.f. = 12, $p = 0.73$).

(c) *Parent–offspring phenotypic correlations*

As expected, yearling males were heavier than females and early-born goats were heavier than late-born ones (table 1). None of the maternal characteristics examined affected offspring mass for either gender when accounting for birth date in a sample of 38 yearlings (17 daughters and 21 sons) from five cohorts and born to 28 mothers (table 1). When the effects of paternal characteristics on off-spring mass were examined together with those of yearling sex and birth date, we found an interaction between paternal mass and yearling sex in a sample of 37 yearlings (16 daughters and 21 sons) from nine cohorts sired by 14 fathers (table 1). The mass of sons increased with paternal mass (figure 3a), whereas that of daughters showed the opposite pattern (figure 3b). Thus, yearling females sired by light males were heavier than yearling males with light fathers (table 1). This interaction remained significant when considering paternal age-specific mass, determined as the deviation from age-predicted mass (Mainguy & Côté 2008; $F = 5.54$, d.f. = 13, $p = 0.03$), with the same trends for sons (figure 3c) and daughters (figure 3d). As this interaction could have been stronger in years with poor conditions for yearling mass gain, we examined whether the interaction 'year × paternal mass' as a random term explained additional variance. As this covariance parameter estimate was equal to 0, we deleted it from the final model, keeping only paternal identity and year as random factors.

Because only 23 yearlings (nine daughters and 14 sons) from 19 mothers and nine fathers had known birth dates and parental masses, we could not fit year as well as
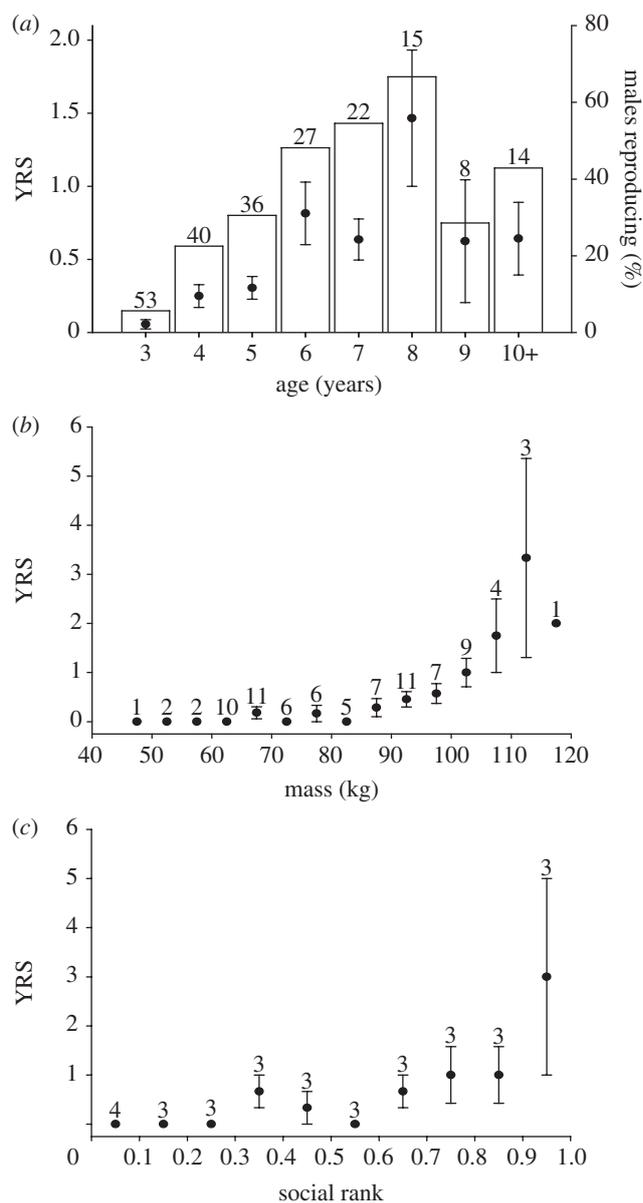
Proc. R. Soc. B (2009)

Figure 2. Mean annual number of kids sired ($\pm$s.e.) that survived to 1 year of age in relation to male (*a*) age, (*b*) mass, and (*c*) social rank in mountain goats at Caw Ridge, Alberta, Canada. Social rank varies from 0 (subordinate) to 1 (dominant). The age-specific percentage of males reproducing (histograms, right *y*-axis) are also shown in (*a*).

maternal and paternal identities as random terms in a single LMM. Therefore, we removed the random term with the lowest level of pseudoreplication (maternal identity) to leave enough degrees of freedom for this analysis. None of the random factors explained significant variance in yearling mass in one-parent analyses, or in this analysis. Despite limited statistical power, this last analysis yielded the same final model as the one presented in table 1, as an interaction between paternal mass and yearling sex best explained the variance in the dependent variable when accounting for birth date (table 2). Using a simple GLM on the same dataset yielded the same results.

(d) *Maintenance of yearling mass to early adulthood*

Body mass at 1 year of age was positively related with mass at 3 years of age in both males ($F = 16.2$,

Table 1. Linear mixed models of the effects of maternal and paternal characteristics, offspring sex and birth date, and the two-way interactions between parental characteristics and sex, on the mass of yearling mountain goats at Caw Ridge, Alberta, Canada. (Estimates for the variable sex or an interaction with it are for females compared with males. Parent identity and year were fitted as random terms.)

variables	β	s.e.	F	d.f.	p
maternal					
sex	−1.80	0.66	7.44	1,15	0.02
birth date	−0.19	0.08	6.18	1,15	0.03
not included in the model					
maternal age × sex	−0.03	0.42	0	1,1	0.96
maternal mass × sex	−0.03	0.10	0.11	1,2	0.77
maternal age	−0.10	0.20	0.28	1,3	0.64
maternal mass	0.08	0.06	1.95	1,3	0.26
paternal					
sex	16.7	7.4	5.05	1,13	0.04
birth date	−0.22	0.08	7.01	1,13	0.02
paternal mass	0.08	0.05	0.11	1,13	0.74
paternal mass × sex	−0.18	0.07	5.98	1,13	0.03
not included in the model					
paternal age × sex	1	0.83	1.46	1,12	0.25
paternal age	0.41	0.32	1.60	1,13	0.23

d.f. = 32, $p = 0.0003$, $r^2 = 0.34$) and females ($F = 6.58$, d.f. = 42, $p = 0.01$, $r^2 = 0.14$).

4. DISCUSSION

We found a strong skew in reproductive success among male mountain goats, as more than half of the kids were sired by less than one-tenth of adult males. Mass was a stronger determinant of male YRS than age or any other trait considered, highlighting the importance of this secondary sexual character for male fitness. Paternal mass was correlated with yearling mass, but in different directions according to gender. These results partly support theory on intralocus sexual conflict (Day & Bonduriansky 2004) and have therefore important implications for females in terms of mate choice. In mountain goats, the reproductive success of both sexes increases with adult mass, although mass has apparently stronger positive effects for males (this study) than for females (Hamel et al. 2009). Thus, given that the influence of paternal mass on offspring mass persists at least until early adulthood, this can have important fitness consequences (Lindström 1999).

Male YRS increased with age until 8 years, when most males reach asymptotic mass, reproductive effort and social rank (Mainguy & Côté 2008; Mainguy et al. 2008). Paternity success decreased for the oldest males, suggesting reproductive senescence as observed in other ungulates (McElligott et al. 2002). Further analyses are, however, required to determine whether the apparent reproductive decline with increasing age could be explained by differential survival of low-quality males (see McCleery et al. (2008) for an example). Mass was also the strongest determinant of male reproductive success in the most sexually dimorphic and polygynous of all mammals, the southern elephant seal (*Mirounga leonina*, Galimberti et al. 2007). Compared to species where males defend harems, however, reproductive skew

on an annual basis is limited in male mountain goats because they only defend one female at a time and oestruses are highly synchronized (94% of matings were observed over 10 days, Mainguy et al. 2008). As predicted (Côté et al. 1998a), horn length had no effect on male reproductive success. The antiparallel fighting style of mountain goats in which horns are used to stab the opponent, sometimes lethally (Geist 1967), may not favour long horns that could break during combat (Festa-Bianchet & Côté 2008). Among the traits considered, mass thus appears to be the only one under positive directional sexual selection. It is important to note that, because we measured male YRS as the number of yearlings sired, our analyses cannot account for a potential influence of paternal alleles on kid survival (Byers & Waits 2006). On the other hand, the number of yearlings sired may better reflect the contribution of each male to the population than the number of kids, as yearling survival is approximately 15 per cent higher than kid survival (Festa-Bianchet & Côté 2008).

Adult females that mated with heavy males apparently gained indirect benefits by producing heavy sons that will probably become heavy adults and enjoy high reproductive success (Hewison & Gaillard 1999; Andersson & Simmons 2006). This pattern, however, was reversed for daughters. Given our limited statistical power to assess the relationship between parental and offspring phenotypes within the same model, these results must be interpreted with caution. On the other hand, the adjusted paternal and maternal masses were based on sex-specific mean growth rates from all adults, as individual growth rates for most goats were unknown. Potential differences in growth among fathers of varying quality were thus not taken into account, possibly reducing the variance in paternal mass and therefore making our results conservative. Nonetheless, our results suggest that paternal alleles coding for heavy mass are advantageous for sons, but may be maladaptive when expressed in daughters. The resulting possible intralocus sexual conflict for body mass could thus potentially mitigate the indirect benefits gained from sexual selection (Pischedda & Chippindale 2006), as this sexually dimorphic shared trait is under positive selection in both genders for reproduction. Thus, daughters of reproductively successful males may have reduced reproductive success owing to their light mass (Hamel et al. 2009), although such parent–offspring fitness relationships remain to be quantified. Recently, Foerster et al. (2007) reported a negative genetic correlation between the fitness of fathers and daughters in red deer, as males with high fitness sired on average daughters with low fitness. Red deer mothers, however, appear to adjust maternal investment to partly counter the effects of paternal alleles (Foerster et al. 2007). Accordingly, Byers & Waits (2006) showed that female pronghorns (*Antilocapra americana*) compensated for mating with non-preferred males by increasing milk transfer compared with females that mated with attractive males. Although females may invest more in sons than in daughters because of the potential higher fitness returns of sons in sexually dimorphic ungulates (Hewison & Gaillard 1999), it remains unknown whether they can modulate this investment according to their mating partner's characteristics. Nevertheless, paternal mass had a detectable effect on offspring mass
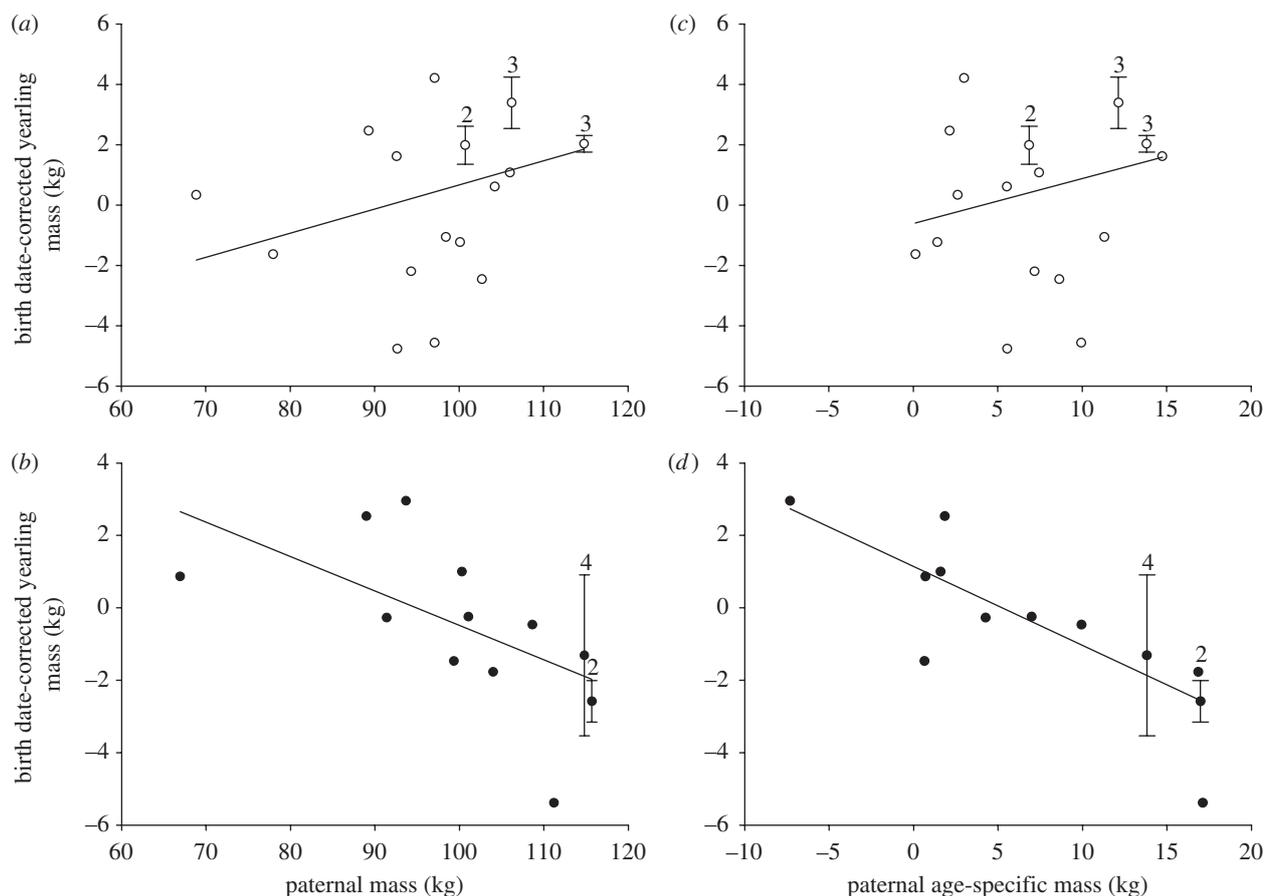
Figure 3. Birth date-corrected residuals of mass (adjusted to 15 July) of yearling males (top, empty circles) and females (bottom, filled circles) in relation to (a,b) paternal mass adjusted on 15 July and (c,d) age-specific adjusted paternal mass, in mountain goats at Caw Ridge, Alberta, Canada. Means ± s.e. are shown when yearlings of the same sex were sired by the same male during the same year, with sample size indicated above error bars.

Table 2. Linear mixed model of the effects of parental masses, sex, birth date and the two-way interactions between parental masses, and parental masses and sex, on the mass of yearling mountain goats at Caw Ridge, Alberta, Canada. (Estimates for the variable sex or an interaction with it are for females compared with males. Paternal identity and year were fitted as random terms.)

variables	β	s.e.	F	d.f.	p
sex	16.7	7.4	5.05	1,13	0.04
birth date	−0.22	0.08	7.01	1,13	0.02
paternal mass	0.08	0.05	0.11	1,13	0.74
paternal mass × sex	−0.18	0.07	5.98	1,13	0.03
not included in the model					
maternal mass × paternal mass	−0.001	0.007	0.03	1,4	0.88
maternal mass × sex	0.08	0.17	0.24	1,5	0.64
maternal mass	0.04	0.09	0.19	1,6	0.68

at 1 year of age, either owing to paternal inherited alleles, mediated maternal non-genetic effects, or both.

Recently, Calsbeek & Bonneaud (2008) have shown negative genetic correlations between the body size of the parent and their opposite-sex offspring in the sexually dimorphic brown anole (*Anolis sagrei*), while positive genetic correlations were found between the parent and same-sex offspring. Our results are similar to these,

although we did not find similar mother–offspring relationships in mountain goats. In another study, Poissant *et al.* (2008) did not find evidence of sexual antagonism for body mass and horn size in the highly sexually dimorphic bighorn sheep (*Ovis canadensis*). Thus, additional studies are required to document the occurrence of sexual conflict for shared traits in the wild and investigate its role in shaping the phenotypes of both genders under sexual selection (Bonduriansky & Chenoweth 2009). In a recent review, Cox & Calsbeek (2009) reported that sexually antagonistic selection for homologous traits was quite common and that intralocus sexual conflict could still persist despite the evolution of sexual dimorphism. In mountain goats, sex-specific selective pressures on body mass are not opposite in sign, but apparently vary in intensity, as this trait seems under greater sexual selection in males than in females. Although this pattern has been observed elsewhere (Cox & Calsbeek 2009), it complicates the interpretation of sexual dimorphism in the context of intralocus sexual conflict because the selective forces acting on body mass for reproduction are in the same direction, i.e. there is a lack of sexually antagonistic selection. Bonduriansky & Chenoweth (2009) noted, however, that intralocus sexual conflict could still prevail under sexually concordant selection, although only when the selection surfaces differ between the sexes, because selection on one sex slows or impedes adaptive evolution in the other sex—a possible situation in mountain goats. To mitigate such 'unresolved' intralocus sexual conflict, selection

should theoretically favour reduced expression of the between-sex component of trait heritability (Day & Bonduriansky 2004). Our findings in mountain goats, as well as those in the brown anole (Calsbeek & Bonneaud 2008), provide empirical support for this. The calculation of selection gradients for sexual, fecundity and viability selection will however be required to further disentangle the forces shaping the sexual dimorphism observed in mass in mountain goats. For instance, identifying the constraints maintaining the lower mass of females compared with males remains an open question. Possibly, strong stabilizing viability selection on body mass (Bouteiller-Reuter & Perrin 2005), which could probably be imposed by the harsh winter conditions met in mountainous environments, could prevent females (and males) from attaining their phenotypic mass optima for reproduction. Another possibility is that paternal alleles may have sexually antagonistic effects on condition, therefore affecting growth rates in offspring differently. This could potentially explain the unusual negative covariance found between fathers and daughters for body mass in mountain goats. Because the expression of sexual dimorphism can be condition dependent (Bonduriansky 2007; Bonduriansky & Chenoweth 2009), genes affecting the efficiency of acquiring and converting resources into fitness in variable environments could have different phenotypic outcomes in males and females, as these are under differential sexual selective pressures. This would definitely merit further investigation in an attempt to elucidate the mechanism(s) behind intralocus sexual conflict, as well as its resolution.

Overall, we showed that mass was the strongest determinant of male reproductive success in mountain goats and the effects of paternal mass on yearling mass were opposite according to sex. To better understand how sexual selection affects offspring phenotypic quality in polygynous mammals, we should further examine the potential interactions between paternal and offspring phenotypes stemming from a genetic basis, and the possibility of skewed maternal care according to paternal characteristics and offspring gender. The 'animal model' (Kruuk 2004) offers a promising approach to assess the quantitative genetics of sexual dimorphism because it can partition parental genetic and non-genetic effects on morphological and fitness traits (Fairbairn & Roff 2006). That technique, however, requires a more complete pedigree than what is currently available for the Caw Ridge population (Mainguy *et al.* 2009). Nevertheless, divergent father–offspring phenotypic correlations, probably stemming from a genetic basis, could contribute to maintaining sexual dimorphism in mass, possibly through sexually antagonistic effects on condition. Sex-specific correlations could also explain part of the substantial variation found for this homologous trait within the two sexes in polygynous mammals, ultimately affecting lifetime breeding success in each gender differently and thus potentially driving adaptive evolution in the two sexes (Bonduriansky & Chenoweth 2009).

The study meets the terms of the ethics committee at the institution and in the country where the experiment was carried out. The project was approved by the Animal Care Committee of Université Laval, affiliated to the Canadian Council on Animal Care.

REFERENCES

Andersson, M. & Simmons, L. W. 2006 Sexual selection and mate choice. *Trends Ecol. Evol.* **6**, 296–302. (doi:10.1016/j.tree.2006.03.015)

Bonduriansky, R. 2007 The evolution of condition-dependent sexual dimorphism. *Am. Nat.* **169**, 9–19. (doi:10.1086/510214)

Bonduriansky, R. & Chenoweth, S. F. 2009 Intralocus sexual conflict. *Trends Ecol. Evol.* **24**, 280–288. (doi:10.1016/j.tree.2008.12.005)

Bonduriansky, R. & Rowe, L. 2005 Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in *Prochyliza xanthostoma* (Diptera: Piophilidae). *Evolution* **59**, 1965–1975.

Bouteiller-Reuter, C. & Perrin, N. 2005 Sex-specific selective pressures on body mass in the greater white-toothed shrew, *Crocidura russula*. *J. Evol. Biol.* **18**, 290–300. (doi:10.1111/j.1420-9101.2004.00836.x)

Bro-Jørgensen, J. 2002 Overt female mate competition and preference for central males in a lekking antelope. *Proc. Natl Acad. Sci. USA* **99**, 9290–9293. (doi:10.1073/pnas.142125899)

Byers, J. A. & Waits, L. P. 2006 Good genes sexual selection in nature. *Proc. Natl Acad. Sci. USA* **103**, 16 343–16 345. (doi:10.1073/pnas.0608184103)

Byers, J. A., Wiseman, P. A., Jones, L. & Roffe, T. J. 2005 A large cost of female mate sampling in pronghorn. *Am. Nat.* **166**, 661–668. (doi:10.1086/497401)

Calsbeek, R. & Bonneaud, C. 2008 Postcopulatory fertilization bias as a form of cryptic sexual selection. *Evolution* **62**, 1137–1148. (doi:10.1111/j.1558-5646.2008.00356.x)

Chippindale, A. K., Gibson, J. R. & Rice, W. R. 2001 Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proc. Natl Acad. Sci. USA* **98**, 1671–1675. (doi:10.1073/pnas.041378098)

Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T. & Strobeck, C. 2002 Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. Lond. B* **269**, 165–172. (doi:10.1098/rspb.2001.1851)

Côté, S. D. 2000 Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* **137**, 1541–1566. (doi:10.1163/156853900502718)

Côté, S. D. & Festa-Bianchet, M. 2001*a* Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**, 230–238. (doi:10.1007/s004420000584)

Côté, S. D. & Festa-Bianchet, M. 2001*b* Reproductive success in female mountain goats: the influence of age and social rank. *Anim. Behav.* **62**, 173–181. (doi:10.1006/anbe.2001.1719)

Côté, S. D. & Festa-Bianchet, M. 2001*c* Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). *Behav. Ecol. Sociobiol.* **49**, 260–265.

Côté, S. D., Festa-Bianchet, M. & Smith, K. G. 1998*a* Horn growth in mountain goats (*Oreamnos americanus*). *J. Mammal.* **79**, 406–414. (doi:10.2307/1382971)

Côté, S. D., Festa-Bianchet, M. & Fournier, F. 1998*b* Life-history effects of chemical immobilization and radio-collars on mountain goats. *J. Wildl. Manage.* **62**, 745–752. (doi:10.2307/3802351)

Cox, R. M. & Calsbeek, R. 2009 Sexually antagonistic selection, sexual dimorphism, and the resolution of intra-locus sexual conflict. *Am. Nat.* **173**, 176–187. (doi:10.1086/595841)

Day, T. & Bonduriansky, R. 2004 Intralocus sexual conflict can drive the evolution of genomic imprinting. *Genetics* **167**, 1537–1546. (doi:10.1534/genetics.103.026211)

Ellis, S. L., Don Bowen, W., Boness, D. J. & Iverson, S. J. 2000 Maternal effects on offspring mass and stage of development at birth in the harbor seal, *Phoca vitulina*. *J. Mammal.* **81**, 1143–1156. (doi:10.1644/1545-1542(2000)081<1143:MEOOMA>2.0.CO;2)

Fairbairn, D. J. & Roff, D. A. 2006 The quantitative genetics of sexual dimorphism: assessing the importance of sex-linkage. *Heredity* **97**, 319–328. (doi:10.1038/sj.hdy.6800895)

Fedorka, K. M. & Mousseau, T. A. 2004 Female mating bias results in conflicting sex-specific offspring fitness. *Nature* **429**, 65–67. (doi:10.1038/nature02492)

Festa-Bianchet, M. & Côté, S. D. 2008 *Mountain goats: ecology, behavior, and conservation of an alpine ungulate*. Washington, DC: Island Press.

Fisher, D. O. & Cockburn, A. 2006 The large-male advantage in brown antechinuses: female choice, male dominance, and delayed male death. *Behav. Ecol.* **17**, 164–171. (doi:10.1093/beheco/arj012)

Foerster, K., Coulson, T., Sheldon, B. C., Pemberton, J. M., Clutton-Brock, T. H. & Kruuk, L. E. B. 2007 Sexually antagonistic genetic variation for fitness in red deer. *Nature* **447**, 1107–1110. (doi:10.1038/nature05912)

Gaillard, J.-M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. 2000 Body mass and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. Lond. B.* **267**, 471–477. (doi:10.1098/rspb.2000.1024)

Galimberti, F., Sanvito, S., Braschi, C. & Boitani, L. 2007 The cost of success: reproductive effort in male southern elephant seals (*Mirounga leonina*). *Behav. Ecol. Sociobiol.* **62**, 159–171. (doi:10.1007/s00265-007-0450-y)

Geist, V. 1967 On fighting injuries and dermal shields of mountain goats. *J. Wildl. Manage.* **31**, 192–194. (doi:10.2307/3798378)

Gendreau, Y., Côté, S. D. & Festa-Bianchet, M. 2005 Maternal effects on post-weaning physical and social development in juvenile mountain goats (*Oreamnos americanus*). *Behav. Ecol. Sociobiol.* **58**, 237–246. (doi:10.1007/s00265-005-0938-2)

Hamel, S., Gaillard, J.-M., Festa-Bianchet, M. & Côté, S. D. 2009 Individual quality, early life environment and reproductive success in contrasted populations of large herbivores. *Ecology* **90**, 1981–1995. (doi:10.1890/08-0596.1)

Haviernick, M., Côté, S. D. & Festa-Bianchet, M. 1998 Immobilization of mountain goats with xylazine and reversal with idazoxan. *J. Wildl. Dis.* **34**, 342–347.

Hegyi, G., Rosivall, B. & Török, J. 2006 Paternal age and offspring growth: separating the intrinsic quality of young from rearing effects. *Behav. Ecol. Sociobiol.* **60**, 672–682. (doi:10.1007/s00265-006-0211-3)

Hewison, A. J. M. & Gaillard, J.-M. 1999 Successful sons or advantaged daughters? The Trivers–Willard model and sex-biased maternal investment in ungulates. *Trends Ecol. Evol.* **14**, 229–234. (doi:10.1016/S0169-5347(99)01592-X)

Kalinowski, S. T., Taper, M. L. & Marshall, T. C. 2007 Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**, 1099–1106. (doi:10.1111/j.1365-294X.2007.03089.x)

Komers, P. E., Birgersson, B. & Ekvall, K. 1999 Timing of estrus in fallow deer is adjusted to the age of available mates. *Am. Nat.* **153**, 431–436. (doi:10.1086/303185)

Kruuk, L. E. B. 2004 Estimating genetic parameters in natural populations using the 'animal model'. *Phil. Trans. R. Soc. Lond. B* **359**, 873–890. (doi:10.1098/rstb.2003.1437)

Kruuk, L. E. B., Slate, J., Pemberton, J. M., Brotherstone, S., Guinness, F. E. & Clutton-Brock, T. 2002 Antler size in red deer: heritability and selection but no evolution. *Evolution* **56**, 1683–1695.

Lidgard, D. C., Boness, D. J., Don Bowen, W. & McMillan, J. I. 2005 State-dependent male mating tactics in the grey seal: the importance of body size. *Behav. Ecol.* **16**, 541–549. (doi:10.1093/beheco/ari023)

Lindström, J. 1999 Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**, 343–348. (doi:10.1016/S0169-5347(99)01639-0)

Littell, R. C., Henry, P. R. & Ammerman, C. B. 1998 Statistical analysis of repeated measures data using SAS procedures. *J. Anim. Sci.* **76**, 1216–1231.

Littell, R. C., Pendergast, J. & Natarajan, R. 2000 Modelling covariance structure in the analysis of repeated measures data. *Statist. Med.* **19**, 1793–1819. (doi:10.1002/1097-0258(20000715)19:13<1793::AID-SIM482>3.0.CO;2-Q)

Mainguy, J. 2008 *Variabilité génétique et reproduction des mâles chez la chèvre de montagne*. Québec, Canada: Université Laval.

Mainguy, J. & Côté, S. D. 2008 Age- and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. *Behav. Ecol. Sociobiol.* **62**, 935–943. (doi:10.1007/s00265-007-0517-9)

Mainguy, J., Llewellyn, A. S., Worley, K., Côté, S. D. & Coltman, D. W. 2005 Characterization of 29 polymorphic artiodactyl microsatellite markers for the mountain goat (*Oreamnos americanus*). *Mol. Ecol. Notes* **5**, 809–811. (doi:10.1111/j.1471-8286.2005.01071.x)

Mainguy, J., Côté, S. D., Cardinal, E. & Houle, M. 2008 Mating tactics and mate choice in relation to age and social rank in male mountain goats. *J. Mammal.* **89**, 626–635. (doi:10.1644/07-MAMM-A-234R.1)

Mainguy, J., Côté, S. D. & Coltman, D. W. 2009 Multilocus heterozygosity, parental relatedness and individual fitness components in a wild mountain goat, *Oreamnos americanus* population. *Mol. Ecol.* **18**, 2297–2306. (doi:10.1111/j.1365-294X.2009.04197.x)

McCleery, R. H., Perrins, C. M., Sheldon, B. C. & Charmantier, A. 2008 Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proc. R. Soc. B* **275**, 963–970. (doi:10.1098/rspb.2007.1418)

McElligott, A. G., Altwegg, R. & Hayden, T. J. 2002 Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). *Proc. R. Soc. Lond. B* **269**, 1129–1137. (doi:10.1098/rspb.2002.1993)

Pelletier, F. & Festa-Bianchet, M. 2006 Sexual selection and social rank in bighorn rams. *Anim. Behav.* **71**, 649–655. (doi:10.1016/j.anbehav.2005.07.008)

Pischedda, A. & Chippindale, A. K. 2006 Intralocus sexual conflict diminishes the benefits of sexual selection. *Publ. Lib. Sci. Biol.* **4**, 2099–2103.

Poissant, J., Wilson, A. J., Festa-Bianchet, M., Hogg, J. T. & Coltman, D. W. 2008 Quantitative genetics and sex-specific selection on sexually dimorphic traits in bighorn sheep. *Proc. R. Soc. B* **275**, 623–628. (doi:10.1098/rspb.2007.1361)

Røed, K. H., Holand, Ø., Mysterud, A., Tverdal, A., Kumpula, J. & Nieminen, M. 2007 Male phenotypic quality influences offspring sex ratio in a polygynous ungulate. *Proc. R. Soc. B* **274**, 727–733. (doi:10.1098/rspb.2006.0214)

SAS Institute 2003 *SAS/STAT user's guide*, version 9.1. Cary, NC: SAS Institute Inc.

Weckerly, F. W. 1998 Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* **79**, 33–52. (doi:10.2307/1382840)